Ruminants from the Miocene of Saudi Arabia

A. W. Gentry

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Synopsis

Six ruminant species have been identified from the Miocene of Ad Dabtiyah, Saudi Arabia. These comprise two tragulids belonging to *Dorcatherium*, the giraffoid *Canthumeryx*, and *Eotragus* and two other bovid species. The tragulid teeth, known only from the smaller of the two species, are well worn. This fauna seems to date from the early Middle Miocene, which would be the later Orleanian or earliest Astaracian of the European scale.

Introduction

The ruminant fossils to be described in this paper come from Miocene continental deposits thought to be laterally equivalent to the Dam Formation, at Ad Dabtiyah, Saudi Arabia. This locality is situated at $26^{\circ} 27' 02'' N$, $48^{\circ} 35' 24'' E$. Further details are given in Hamilton *et al.* (1978) and Whybrow *et al.* (this issue, p. 375).

Register numbers of individual specimens refer to the collection of the British Museum (Natural History), London.

Systematics

Order ARTIODACTYLA Owen, 1848

Infraorder TRAGULINA Flower, 1883

Family TRAGULIDAE Milne Edwards, 1864

Genus DORCATHERIUM Kaup, 1833

Dorcatherium sp. Figs 46, 48D

Some tragulid remains from Ad Dabtiyah are about the size of *Dorcatherium pigotti* Whitworth (1958: 9) of the east African early Miocene and *Dorcatherium* sp. of Colbert (1935: 311) of the Siwaliks Group, Pakistan. They are smaller than *D. libiensis* Hamilton (1973: 80; pl. 1, fig. 1) from Gebel Zelten, Libya. The first is part of a fragmentary right mandible with P_2 and P_3 , M.34278 (Fig. 46C), in which P_3 and the back of P_2 are well worn. The occlusal lengths of P_2 and P_3 are 6.5 and 8.5 mm respectively.

Two pieces of right mandibles (Fig. 46D, E) also show M_2 (M.34279a) and M_{3} s (both M.34279a and b) in late wear. What can be discerned of the occlusal pattern on the M_{3} s does not look like a pecoran. The central cavities have wide posterior openings to the outside and the labial lobes are insufficiently narrow and pointed. They lack basal pillars and are thus unlike *D. libiensis*. The occlusal lengths of the M_3 s are 12.8 and 13.2 mm.

Three right upper molars and two right upper molars, M.30131 (Fig. 46A) and M.30132 respectively, belong to a tragulid of similar size to the above pieces. They are very well worn. They have a cingulum around the lingual lobes, especially the anterior one, as is usual in tragulids. The posterolabial rounding of the anterior lingual lobe (protocone) also looks tragulid rather than pecoran. The rib between parastyle and mesostyle is less deflected anteriorly than in the Siwaliks *Dorcatherium* of Colbert (1935: figs 138, 141, 143), which perhaps indicates that the Arabian fossils are geologically older. The occlusal lengths of M¹ and M³ in M.30131 are 8.3 and 9.7 mm; the two upper molars in M.30132 measure 8.7 mm (front one) and 9.1 mm (rear one).

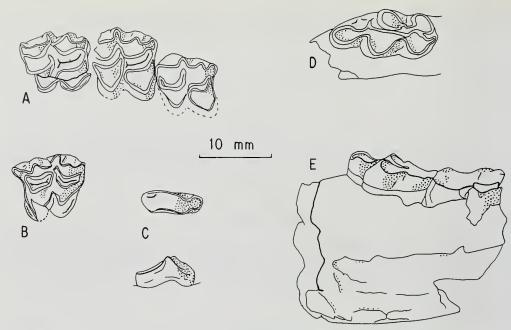


Fig. 46 Teeth of *Dorcatherium* from Ad Dabtiyah. Anterior side to right (except B). A, occlusal view of right M¹⁻³, M.30131. B, occlusal view of left dP⁴, M.30133. C, occlusal and lateral views of right P₃, M.34278. D, occlusal view of right M₃ in mandible, M.34279b. E, lateral view of another right mandible with M₂₋₃, M.34279a.

M.30133 is a left dP^4 in late middle wear with an occlusal length of 9.3 mm (Fig. 46B). It has a notably large parastyle and a cingulum on its lingual lobes. The strong parastyle and the convergent front and back walls of the tooth suggest it is a dP^4 and not a molar.

Thomas et al. (1982: 127) have reported a similar-sized Dorcatherium from Al-Sarrar.

A right and a left astragalus (M.35265; M.35266, Fig. 48D), a left naviculocuboid plus ectocuneiform (M.35267) and a proximal left metatarsal (M.35268) have tragulid morphology and are about the size of *D. pigotti.*

Dorcatherium, larger sp. Fig. 48A–C

A further left astragalus, M.35269 (Fig. 48C), is larger than those assigned to the above *Dorcatherium* sp. and matches the size of *D. chappuisi* Arambourg of the east African early Miocene (see Whitworth 1958: 4). Much of a left tibia including the distal end, M.35079 (Fig. 48A, B), could also belong here. It is larger than the tibia of the living *Hyemoschus aquaticus* and the distal articular facet is longer anteroposteriorly and less wide transversely. These proportions are nearer to those of Suidae and therefore presumably nearer to the ancestral state. The total length of the tibia would have been in the region of 150 mm.

Infraorder PECORA Linnaeus, 1758

Superfamily GIRAFFOIDEA Simpson, 1931

Genus CANTHUMERYX Hamilton, 1973

Canthumeryx sp. Fig. 48E

A much damaged but practically complete giraffoid left metatarsal, M.34277, is about 320-330 mm long and about 36 mm wide across its distal condyles. It is close in size to the

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metatarsal of *Canthumeryx sirtensis* Hamilton from Moruorot, Kenya (Arambourg 1947: pl. 22, fig. 5; Hamilton 1978: 178) but about 25%-30% longer and thereby presumably more advanced. It is too gracile to belong to a *Palaeomeryx* such as that known from Sansan, France.

A left unciform, M.35078 (Fig. 48E), is also of an appropriate size to belong to *Canthumeryx*. Compared with modern Bovidae it shows more resemblance to Tragelaphini than to Alcelaphini, in that the back of the facet for the cuneiform is less deeply excavated towards the ventral edge of the bone, and also in that there are separate dorsal and ventral facets on the posterior part of the medial side. It differs from examples of extant giraffids, cervids and bovids in having a prominent downturned flange posteriorly.

Thomas et al. (1982: 124) recorded a probable Canthumeryx from the Al-Sarrar locality. They illustrated an upper molar (1982: pl. 116, fig. 5) on which the rather bulky condition of styles and anterior rib are presumably owing to late wear. They draw attention to the difficulty in identifying giraffoids from isolated upper teeth. Among their other remains was a metacarpal with a length and distal condylar width of 360 mm and 38 mm respectively. According to Pickford (1981: 96) Canthumeryx belongs to 'Set II' faunas in east Africa, dating from 18.5-16.5 Ma and possibly to 'Set III' ones at 16.5-14.5 Ma. It is zoogeographically interesting that the mandible with M_{2-3} of *Progiraffa exigua* from Dera Bugti (Pilgrim 1911: pl. 1, fig. 1) looks as if it could be congeneric with Canthumeryx (as Hamilton had independently recognized-Patterson 1981: 462). This slightly later faunal element contrasts with the antique aspect of most of the Bugti mammals and perhaps came from a higher level; Pilgrim (1912: 2) and Pascoe (1964: 1656) refer to bones in the deposit being scattered through most of its thousandfoot (305 m) thickness. Canthumeryx precedes and may be ancestral to Giraffokeryx Pilgrim, and also to pre-Hipparion representatives of Palaeotragus Gaudry which Hamilton (1978: 200) believed to be not congeneric with the type species P. roueni. Canthumeryx is unknown from Europe.

Superfamily BOVOIDEA Simpson, 1931

Family BOVIDAE Gray, 1821

Genus EOTRAGUS Pilgrim, 1939

Eotragus sp. Figs 47A, 48F

This is represented by M.30134, a left P_3 , P_4 and M_1 in early wear and with occlusal lengths 9.3, 11.1 and 12.0 mm respectively (Fig. 47A). The central parts of the M_1 are missing. The size and proportions of the teeth would be similar to Protragocerus Depéret, e.g. P. labidotus Gentry (1970: 247) of Fort Ternan, except that they are lower-crowned and the basal pillar on the molar is smaller, both of which make them like *Eotragus* as illustrated in Thenius (1952). A trace of an anterior cingulum on the molar is like both *Eotragus* and *P. gluten* (Pilgrim) of the Siwaliks. The premolars match Eotragus and Protragocerus in that the anterolabial wall is not turned to lie in a transverse plane, in the diagonal alignment of the metaconid, and in the weak differentiation of a paraconid. The molar is about the size of a bovid lower molar from Maboko, Kenya (Whitworth 1958: Fig. 10a-c), but the labial lobes may be more narrowly pointed. The teeth are a little larger and higher-crowned than in the bovid-like pecoran Walangania africanus (Whitworth 1958) from the east African early Miocene (Hamilton 1973: 146), and the molar has a smaller basal pillar, no diagonal fold on the rear wall of the protoconid (Palaeomeryx fold), a weaker metastylid and a weaker anterior rib on its lingual wall. A probable bovid from Arrisdrift, Namibia (Hendey 1978: fig. 12) is smaller and has quite a strong paraconid on its P_4 .

Eotragus is the most likely identity for M.30134. This genus is known in Europe from the Orleanian and Astaracian (MN 4–7 of Mein 1975, 1979). It also appears to be represented at Gebel Zelten, Libya by horn cores M.26688 and M.26689 (Hamilton 1973: 127; pl. 13, fig. 1), and comes in at Maboko in the east African succession of Miocene faunas with a cranial roof

M.15544 (Gentry 1970: 303; Thomas 1979: 296). It may be present at the later Fort Ternan locality (Gentry 1970: 261; pl. 15, figs 6, 7). Pickford (1981: 96) has Maboko as one of his 'Set III' faunas with a probable age back to 16.5 Ma.

A partial right horn core of a bovid, M.34270, has only the anterior part of its base preserved, along with the supraorbital pit and part of the frontal. Its insertion angle is inclined backwards at about the same angle as in *Eotragus*. The supraorbital pit is narrow. Not enough is left of the horn core above the pedicel for definite identification as *Eotragus*.

The greater part of a left astragalus, M.34271 (Fig. 48F), rather larger than in *Walangania*, could also belong to the same species as M.30134.

Bovidae, Genera indet.

Bovid species 2 Fig. 47B

The back part of an unworn right M_3 , M.34272, looks like a bovid and comes from a larger species than M.30134. It is like M.42005, the back of an M_3 identified as cf. *Oioceros* sp. and coming from Jabal Midra ash-Shamali in the Hadrukh Formation (Whybrow *et al.* 1982: 110). It is smaller than M.42005 but about as hypsodont. Further, the entostylid part of the middle lobe on the lingual side of the tooth is at a markedly lower level than the entoconid constituting the rest of this lobe, a character unlike other bovids but probably present in M.42005.

Bovid species 3 Figs 47C–F, 48G–K

The back of a right M_3 , M.34273 (Fig. 47C), is in early middle wear and may belong to a species smaller than M.30134 and about the size of the bovid from the Dam Formation at Al-Sarrar (Thomas *et al.* 1982: 126; pl. 116, figs 6, 7). It is about as high-crowned as *Eotragus*.

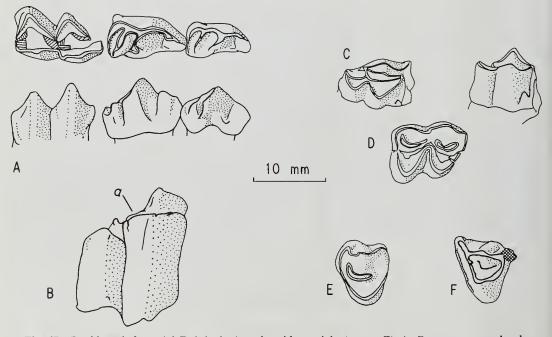


Fig. 47 Bovid teeth from Ad Dabtiyah. Anterior side to right (except E). A, *Eotragus* sp., occlusal and medial views of left P₃-M₁, M.30134. B, bovid sp. 2, lateral-occlusal view of back part of right M₃, M.34272; a indicates low entostylid behind entoconid. C-F, bovid sp. 3. C, occlusal and lateral views of back part of right M₃, M.34273. D, occlusal view of right lower molar, M.34274. E, occlusal view of left P⁴, M.34275. F, occlusal view of right P⁴, M.34276.

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The hypoconulid, or the main part of the rear lobe, has a flat lingual wall. A flange, present at its posterior end, does not loop round anteriorly to meet the entostylid or entoconulid and thus enclose a central cavity. This makes the specimen unlike *Walangania* but more like most *Eotragus* and the Arrisdrift, Namibia (Hendy 1978) species. But its condition is not like the early *Eotragus* which at Artenay, France (Ginsburg & Heintz 1968; pl. 1, figs 4a, b) has a completely enclosed central cavity. The entostylid of M.34273 is less large than in the Arrisdrift specimen. The central cavity on the second lobe does not open to the exterior posteriorly.

Thomas *et al.* (1982: 126) suggested that the Al-Sarrar bovid was congeneric if not conspecific with the Arrisdrift species. However, it can be seen from their figure (1982: pl. 116, fig. 6) that P_{3-4} are about as long as in the Arrisdrift specimen whereas M_{1-3} is considerably longer. From my own measurements the premolar row length would have been around 75% of that of the molar row length in the Arrisdrift specimen whereas on the two illustrated Al-Sarrar specimens the same ratio is around 61%. It is thus unlikely that they could be conspecific.

A right lower molar in middle wear with an occlusal length of 9.5 mm, M.34274 (Fig. 47D), could also belong to the same species. It is smaller than the M₁ of M.30134 and is close in size to the molars of *Gazella* from Gebel Zelten (Hamilton 1973: 128; pl. 13, figs 2, 3). It has transversely long labial lobes, a tiny basal pillar, and may be higher-crowned than M.30134.

A left P^4 in middle wear, M.34275 (Fig. 47E), has an occlusal length of 7.1 mm and a right P^4 in early wear, M.34276 (Fig. 47F), has an occlusal length of c. 7.8 mm. They are low-crowned but smaller than *Eotragus*. The second can be seen to differ from *Eotragus* by its stronger metastyle and stronger rib in front of it, and by a narrower lingual part of the tooth. The last feature is presumably primitive.

A proximal right tibia, M.35080 (Fig. 48G, H), smaller than Protragocerus labidotus (Gentry

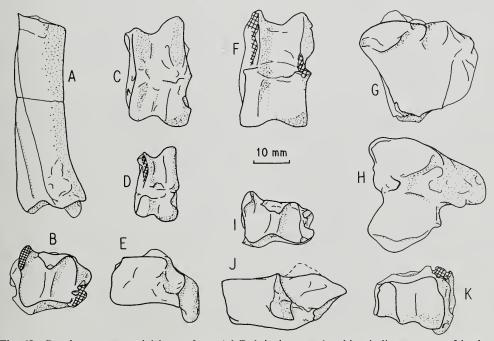


Fig. 48 Ruminant postcranial bones from Ad Dabtiyah; cross-hatching indicates areas of broken bone. A-C, Dorcatherium, larger sp. A, medial view of distal left tibia, M.35079. B, articular surface of same, anterior side towards top. C, anterior view of left astragalus, M.35269. D, Dorcatherium sp., anterior view of left astragalus, M.35266. E, Canthumeryx sp., lateral view of left unciform, M.35078. F, ?Eotragus sp., anterior view of left astragalus, M.34271. G-K, bovid species 3. G, lateral view of proximal right tibia, M.35080. H, articular surface of same, anterior side towards right. I, articular surface of distal left tibia, M.35070, anterior side towards top. J, medial view of partial left calcaneum, M.35071. K, anterior view of distal right humerus, M.35074.

1970: pl. 11, fig. 2) or *Walangania*, may also be of this species. It shows boselaphine or possibly primitive characters like *P. labidotus* in that there is only a shallow hollowing between the two flanges in the centre of the top articular surface, there is little differentiation of a tubercle and medial hollow in the area in front of the flanges, and the lateral edge of the lateral facet is not upwardly turned. A distal left tibia, M.35070 (Fig. 481), has an anterior as well as a posterior facet for the fibula.

Three partial calcanea, M.35071-3 (Fig. 48J), look pecoran but come from animals smaller than *Walangania*. A distal right humerus, M.35074 (Fig. 48K), could also be of the same species.

Either or both of two first phalanges, M.35081-2, also belong to a species smaller than *Walangania africanus*. The central groove on the proximal articular surface passes completely to the front edge of the bone. In this they look fully pecoran, i.e. more advanced over the tragulid condition than in some BM(NH) examples of early Miocene '*Dremotherium*' from Allier, France. Of course it is conceivable that in early pecorans the front and back legs might be different for such a character as this. The Ad Dabtiyah phalanges have at best only indistinct facets at the back of the proximal articular surfaces for the sesamoid bones.

Discussion of ruminant fauna

The tragulid teeth from Ad Dabtiyah are well worn but appear to belong to *Dorcatherium*, first known from the early Miocene (c. 19–20 Ma) of east Africa and probably contemporaneously in Europe. It may also be noted that *Dorcatherium* occurs in the basal Miocene of the upper part of the Nari Formation at Dera Bugti, Pakistan; a cast M.11080 of M_2 - M_3 of 'Gelocus ?qajensis' Pilgrim (1912: pl. 25, fig. 5) is very close or identical to the east African D. chappuisi.

A larger species of *Dorcatherium* is represented by postcranial bones.

Canthumeryx has been recorded, but no remains definitely identifiable as Cervidae.

The main bovid species from Ad Dabtiyah resembles an *Eotragus*; the second and larger species is like the primitive cf. *Oiceros* sp. of the Hadrukh Formation (Whybrow *et al.* 1982: 109); a third probable bovid is smaller than the *Eotragus* and is possibly the same species as that described by Thomas *et al.* (1982: 126) from Al-Sarrar.

Ruminants like these suggest that the fauna dates from before the period of Fort Ternan and is about equivalent to Maboko in the east African Miocene. It would thus be from the early Middle Miocene and would be expected to correspond to later Orleanian or early Astaracian in European terms. This is a more precise temporal placing than was possible with the rhinoceroses (Gentry, this issue, pp. 425, 429) and is later than suggested by the mastodon (Gentry, this issue, p. 406). Thomas *et al.* (1978: 71) and Thomas (1983) record *Protragocerus, Gazella* and *Caprotragoides potwaricus* (Pilgrim) from the Hofuf Formation overlying the Dam Formation. Such an assemblage would match Fort Ternan and kindred sites and gives support for the earlier age suggested for the underlying fauna herein described.

Palaeoecologically it may be noted that *Dorcatherium* is an important constituent of the Kenyan early Miocene communities held by Evans *et al.* (1981: 116) to have inhabited forests. Modern tragulids too are inhabitants of forests. With *Canthumeryx* the difficulty would be to choose between okapi (forest) and giraffe (savanna) as analogues for habitat choice. The appearance of any bovids at all in a Miocene fauna can be held to herald less closed habitats, but only one of the species shows possible beginnings of hypsodonty which could, but need not, be correlated with grazing. Maboko is the African locality with the most similar list of ruminant taxa and here the deduced habitat was woodland (Evans *et al.* 1981: 112).

The ruminants, as well as the mastodon and rhinoceroses described elsewhere in this issue, largely fail to indicate zoogeographical relationships for the Ad Dabtiyah fauna. *Canthumeryx*, being unknown in Europe, would have suggested an African affinity but for the Manchar Formation, Pakistan (Raza *et al.* 1984: 591) and Bugti occurrences of the probably congeneric *Progiraffa exigua*. Detailed study of original material of *Gomphotherium*, *Dicerorhinus*, *Dorcatherium* and perhaps *Eotragus* in various museum collections might, or might not, allow one to discriminate morphologically between allied species living on different continents during the Miocene, but hitherto there has been little consideration of this question.

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